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Review and synthesis

Understanding extinction debts: spatio–temporal scales, mechanisms and a roadmap for future research

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Extinction debt refers to delayed species extinctions expected as a consequence of ecosystem perturbation. Quantifying such extinctions and investigating long-term consequences of perturbations has proven challenging, because perturbations are not isolated and occur across various spatial and temporal scales, from local habitat losses to global warming. Additionally, the relative importance of eco-evolutionary processes varies across scales, because levels of ecological organization, i.e. individuals, (meta) populations and (meta)communities, respond hierarchically to perturbations. To summarize our current knowledge of the scales and mechanisms influencing extinction debts, we reviewed recent empirical, theoretical and methodological studies addressing either the spatio–temporal scales of extinction debts or the eco-evolutionary mechanisms delaying extinctions. Extinction debts were detected across a range of ecosystems and taxonomic groups, with estimates ranging from 9 to 90% of current species richness. The duration over which debts have been sustained varies from 5 to 570 yr, and projections of the total period required to settle a debt can extend to 1000 yr. Reported causes of delayed extinctions are 1) life-history traits that prolong individual survival, and 2) population and metapopulation dynamics that maintain populations under deteriorated conditions. Other potential factors that may extend survival time such as microevolutionary dynamics, or delayed extinctions of interaction partners, have rarely been analyzed. Therefore, we propose a roadmap for future research with three key avenues: 1) the microevolutionary dynamics of extinction processes, 2) the disjunctive loss of interacting species and 3) the impact of multiple regimes of perturbation on the payment of debts. For their ability to integrate processes occurring at different levels of ecological organization, we highlight mechanistic simulation models as tools to address these knowledge gaps and to deepen our understanding of extinction dynamics.

Keywords: Anthropocene, biotic interactions, extinction dynamics, mechanistic modelling, time lag, transient dynamics

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Introduction

Species extinctions after any ecosystem perturbation or disturbance are not all immediate (Box 1). Some populations and metapopulations can persist for extended periods below a minimum viable population size or an extinction threshold (Box 1). These delayed extinctions constitute an extinction debt (Tilman et al. 1994, see Malanson 2008 for a historical overview of the concept). This concept also suggests that extinctions are avoidable if effective conservation measures are implemented (Hanski and Ovaskainen 2002, Kuussaari et al. 2009). Fulfilling this conservation potential, however, depends on our ability to understand the ecological processes upon which conservation measures could act (Cronk 2016). Previous studies have reviewed the evidence of extinction debt in a variety of environments and organisms (Kuussaari et al. 2009, Essl et al. 2015a). Abiotic and biotic factors, such as perturbation intensity and species life-history traits, respectively, as well as stochasticity have been shown to influence how many extinctions happen and how long they will take (Kuussaari et al. 2009). Extinctions involve responses of individuals that scale up to patterns and processes at the population, metapopulation and species levels (Hylander and Ehrlén 2013). At the community (and metacommunity) levels, biotic interactions add further feedbacks between these processes (Jackson and Sax 2010, Essl et al. 2015a). The variety of processes, the ecological level at which they act, and interactions among them complicate the ability to predict which, when and why species go extinct. Understanding this extinction dynamics and the underlying processes is paramount, considering that current extinction debts represent a sizable portion of the predicted 1 million species threatened with extinction (hundreds of thousands of terrestrial species alone – Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) 2019, based on Hoskins et al. 2019).

Extinction debts have been studied mainly via statistical or theoretical models due to a lack of appropriate long-term biodiversity data for estimating or directly quantifying extinctions (Kuussaari et al. 2009, Sodhi et al. 2010, Dornelas et al. 2013, 2018, Vellend et al. 2013). Statistical models can detect extinction debts by verifying whether current species richness exceeds or corresponds to expected values under current habitat conditions (Kuussaari et al. 2009). These

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Box 1. Metrics and components of extinction debt

The extinctions that comprise an extinction debt can be expected based on the assumption of a new equilibrium to be achieved. This new equilibrium is also a community state that depends on how much the perturbation changes environmental conditions and community properties. The changes in species richness will then emerge from the interactions of eco-evolutionary processes over time at multiple levels of ecological organization (Cabral et al. 2017, 2019). This reasoning emphasizes extinction debt as a community (or metacommunity) state. Therefore, we further refer to mechanisms of extinction debt as eco-evolutionary processes creating or prolonging this state, i.e. delaying extinctions and thus putting and maintaining the community into debt.

Being a state, an extinction debt has to be first and foremost, detected. Once detected, it can be characterized (Fig. 1). The extinction debt itself is the number of extinctions expected to happen as consequence of a perturbation, therefore, the main metric is the size or magnitude of the debt. Depending on the strength of the perturbation, immediate extinctions might happen, but most extinctions are usually delayed (a and b in Fig. 1, respectively). Immediate extinctions are mostly relevant for strong pulse perturbations, in which entire species are wiped out by the perturbation itself. Therefore, at the time of perturbation (t_P), the extinction debt coincides with the total number of expected extinctions (a + b if there are no immediate extinctions or b, if there are). As these extinctions happen, during the relaxation time (c in Fig. 1), the second most important metric, the extinction debt decreases. When the relaxation is over (at t_R, with $t_R - t_P$ being the relaxation time, c), the extinction debt is zero, i.e. it is paid.

Other relevant metrics of an extinction debt are the half-life of extinction debt (the time necessary for 50% of the expected extinctions to happen – d in Fig. 1) and the time to first extinction (e, the time necessary for species to fall from S to $S - 1$; Halley et al. 2016).

An important component of extinction debts is the extinction threshold. Derived from a patch-occupancy model (Hanski and Ovaskainen 2002), extinction threshold refers to the metapopulation conditions where the proportion of suitable habitat patches (h) has to be higher than the ratio between a species' colonization and extinction rates (p_c and p_e, respectively – this is a demographically implicit model, therefore the rates are measured in terms of patches being occupied or unoccupied by the species). Therefore, the extinction threshold is defined as $h > p_e/p_c$. Similar to the minimum viable population size, the extinction threshold defines the minimal conditions for metapopulation persistence (number of occupied patches at equilibrium is bigger than zero; Hanski and Ovaskainen 2002).
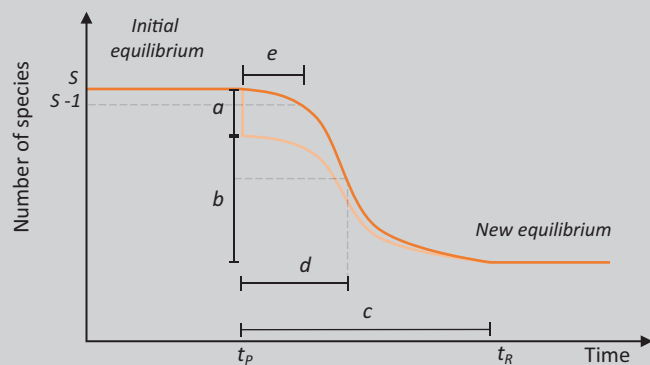

Figure 1. Components of the relaxation process: (a) immediate extinctions, (b) delayed extinctions, (c) relaxation time, (d) half-life of extinction debt, (e) time to first extinction. t_P is the time of perturbation, and t_R, the end of the relaxation time.

statistical models may suggest, but cannot mechanistically detail why, for which species or for how long extinctions are being delayed. Theoretical models, however, provide insights into relevant processes but the development of such models is slow and data-dependent for parameterization and verification (Getz et al. 2018). Mechanistic models have been, therefore, infrequently used to investigate extinction dynamics in real systems (Kuussaari et al. 2009). Nonetheless, upon detection of an extinction debt, conservation efforts must account for dynamic biodiversity change to avoid underestimating its strength, which would render conservation efforts ineffective (Jackson and Sax 2010, Hylander and Ehrlén 2013, Essl et al. 2015a, b). Because the different eco-evolutionary processes associated with biodiversity dynamics are simultaneous (Jackson and Sax 2010, Essl et al. 2015a) and synergistic (Brook et al. 2008), our understanding of the relative roles of these processes remains challenging.

As a consequence of the mechanistic complexity related to extinction debt, recent reviews called for more mechanistic and dynamic frameworks to investigate extinction debts (Kuussaari et al. 2009, Jackson and Sax 2010, Hylander and Ehrlén 2013, Essl et al. 2015a, b). With this review we acknowledge this call and aim to synthesize the contributions of individual studies to better understand eco-evolutionary processes that delay extinction, i.e. those processes that generate extinction debts. We build up on the work of Kuussaari et al. (2009), the most recent review summarizing the challenges in understanding extinction debts; of Hylander and Ehrlén (2013), who emphasize the importance of processes happening at the individual, population and metapopulation levels in generating extinction debts; of Jackson and Sax (2010), who highlight the importance of transient dynamics of biodiversity response to environmental change such as the co-occurrence of extinction debts and immigration credits; and of Essl et al. (2015a), who highlight the contributions of hierarchical processes at different ecological levels and at different rates. First, we present our systematic literature search, with retrieved studies organized into three main categories: 'empirical', 'theoretical' and 'methodological' work. Second, with the aid of empirical and theoretical work, we characterize the range of spatial and temporal scales that extinction debts can reach. Third, we summarize the mechanisms explicitly investigated by empirical and theoretical work that delayed extinctions. Finally, we propose a roadmap for future research, to address the aspects of extinction debts that remain poorly investigated by empirical and theoretical work, particularly with respect to scales and mechanisms. As a navigational tool for this roadmap, we propose eco-evolutionary mechanistic models for their potential to integrate the multiple processes necessary to simulate the dynamics of extinctions from the individual to the metacommunity level.

Overview of literature

Our systematic search returned 397 articles, published between 2009 (year of publication of Kuussaari et al. 2009)

and 2017, from which 114 fulfilled our inclusion criteria (details in Supplementary material Appendix 1 Material and methods). In this section, we summarize the findings from 83 studies in three categories, according to their main focus: A) observational or experimental empirical studies focused on detecting extinction debts in natural systems (hereafter referred to as 'empirical work'); B) theoretical explorations of extinction debt in mathematical or computational models, which may or may not have been validated by empirical data ('theoretical work'); and C) analyses of issues concerning the methodologies used for detecting extinction debts ('methodological work'). We further characterized each paper within these categories in Supplementary material Appendix 1 Table A1–A3. An additional 31 papers found in our search that did not fit into the above categories are discussed throughout this review whenever relevant (and listed in Supplementary material Appendix 1 List A1).

Empirical work

There is a consensus that current biodiversity loss lags behind anthropogenic environmental pressures (Jackson and Sax 2010, Essl et al. 2015a) for several groups of organisms, across the globe (Fig. 2a). Estimates of the size of current extinction debts for natural systems range from 9% to 90% of current local species richness (n = 8). Not included in this range are studies that provided scenario- and/or model-dependent estimates (Wearn et al. 2012, Fordham et al. 2016). Considering a variety of scenarios of forest loss in the Amazon, Wearn et al. (2012) predicted mean local (per 2500 km^2 area) extinction debts of at least 4.88% of vertebrate species by 2050 under the most optimistic scenario, and up to 26.94% under the business-as-usual scenario. Fordham et al. (2016) predicted the loss due to climate change of 16% (under a policy-intervention scenario) and 28% (business-as-usual scenario) of the current 25 species of frogs in the Australian Wet Tropics in the next 200 yr. Depending on the model used to calculate them, however, the extinctions estimated under policy-intervention and business-as-usual scenarios rise up to 20% and 36%, respectively, in the next 80 yr (Fordham et al. 2016). Reported absolute values of extinction debt range from 0.3 to 100 species (Guardiola et al. 2013, Olivier et al. 2013, Chen and Peng 2017). Studies have also measured other biodiversity changes related to extinction debts. Those include predicted range contraction from 44 to 50% for alpine plant species (Dullinger et al. 2012) and predicted range shifts towards inaccessible areas (50% change in distribution area, Pandit et al. 2017). All estimates are listed in Supplementary material Appendix 1 Table A1.

Although we found studies conducted on all continents except Antarctica, the highest concentration of studies were in northern temperate regions, in comparison to tropical areas (Fig. 2a). This reflects the lead of Europe-based researchers in quantifying extinction debts, including cross-country, continent-wide studies (Krauss et al. 2010). One study, however, mapping global estimates of extinction debts and extinction risks for forest-dwelling reptile, mammal and amphibian
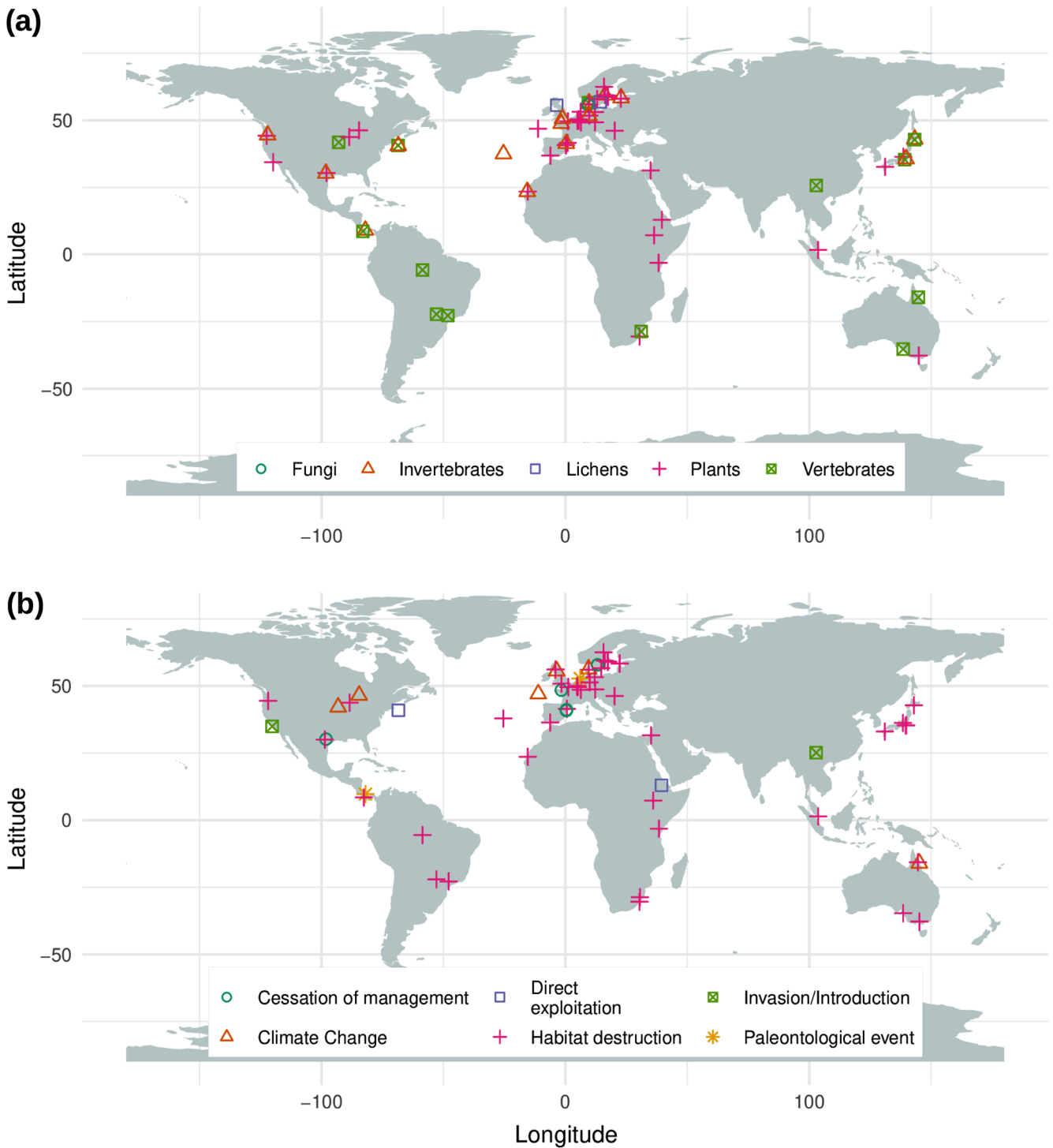
Figure 2. Distribution of (a) taxonomic groups for which extinction debt was investigated and of (b) the causative perturbations behind the possible extinction debts. Both panels include 58 empirical studies investigating extinction debts in real-world systems, published between 2009 and 2017. All studies are listed in Supplementary material Appendix 1 Table A1 in (studies at the continental (n = 2), global (n = 4) or microcosmic (n = 1) scales were not included). Supplementary material Appendix 1 Fig. A2a–b shows the distribution of studies in Europe.

species found areas of high extinction debt in South America, Africa and south Asia (Chen and Peng 2017). Studies in tropical communities have focused equally on plant and vertebrate species, while those in temperate regions have focused on plants and invertebrates (Fig. 2a; but see Dullinger et al. 2013 for a description of extinction risks to vascular plants, bryophytes, mammals, reptiles, dragonflies and grasshoppers across 22 European countries). Habitat destruction

(fragmentation and/or area loss) was the predominant perturbation studied in all regions (Fig. 2b, Supplementary material Appendix 1 Table A1). Few studies have investigated extinction debts in aquatic ecosystems (Duplisea et al. 2016, Pandit et al. 2017, Supplementary material Appendix 1 Table A1), reinforcing calls to address extinction debts when planning conservation of fresh-water (Olden et al. 2010, Hoagstrom et al. 2011, Braulik et al. 2014) and marine environments (Briggs 2011).

While the availability of data on past landscape configuration (e.g. aerial photographs, Krauss et al. 2010) made it possible to standardize past and present landscape metrics, availability of past biodiversity estimates is scarce (Supplementary material Appendix 1 Table A4). Therefore, most studies use regression techniques or comparison of equilibrium numbers of species between disturbed and non-disturbed habitats to explain current biodiversity state (Fig. 3; see Kuussaari et al. 2009 for a summary of the possible methods of estimating extinction debts). Compared to studies from the northern hemisphere, studies conducted in tropical areas have applied a wider variety of alternative methods, such as bioclimatic models coupled with demographically explicit niche models (Fordham et al. 2016, Fig. 3a). Even though a relatively small number of cases have verified the debt of possibly interacting species (n = 7 out of 65 empirical studies, Fig. 3c), even fewer studies explicitly address changes in species interactions (n = 2). This imbalance could be related to the methodological difficulties of quantifying species interactions. To investigate extinction debts, these obstacles were overcome by the use of microcosm experiments (Gibbs and Jiang 2017) and of regression techniques applied to network metrics (Guardiola et al. 2018).

Theoretical work

Theoretical studies have used different ecological theories to conceptualize extinction debt. Besides metapopulation and island biogeography theories, on which the extinction debt concept was based, neutral and niche theories have also been used in a variety of dynamic models, and have ranged from individual-based (Claudino et al. 2015) to purely mathematical models (Chen and Shen 2017). Since each theory clarifies a different aspect of extinction debts, more than one was often combined in the same study (Supplementary material Appendix 1 Table A2).

Island biogeography and metapopulation theories have been used to investigate the impact of habitat fragmentation and/or the role of dispersal capacity on different aspects of the extinction process. Larger fragments are more likely to sustain extinction debts than smaller ones (Kuussaari et al. 2009). However, as species approach the extinction threshold (Box 1), extinction dynamics are similar, independent of fragment size (Huth et al. 2015). The competition–colonization trade-off, historically important for extinction debt studies (Malanson 2008), connects principles of both niche and metapopulation theories. Trade-off models of coexistence show how coexistence mechanisms, interacting with post-perturbation metapopulation dynamics, can give rise to the heterogeneous extinction dynamics that compose an extinction debt (Holt 1993). For example, while direct extinctions happen rapidly, mostly as a result from habitat destruction affecting source–sink dynamics, indirect extinctions take longer and result from habitat destruction that destabilizes coexistence and enables competitive exclusion (Mouquet et al. 2011). Allee effects, an expected feature of decreasing populations (Amarasekare 1998), can invert outcomes of classical experiments on the competition–colonization trade-off (Tilman et al. 1994), with superior colonizers going extinct first if their colonization rate decreases when population size is low (Chen et al. 2009). Moreover, strong Allee effects may render habitat restoration ineffective to prevent extinctions (Labrum 2011).

Despite the importance of niche-based differences demonstrated in the above-mentioned studies, neutral dynamics and stochasticity have been shown to be just as relevant in determining populations' fate after perturbation. For example, ecological drift can neutralize competitive superiority in meta-communities composed of small local communities, because demographic stochasticity becomes a stronger factor in determining species persistence (Orrock and Watling 2010). At the same time, neutral theory makes it possible to identify the relative importance of different processes to extinction dynamics. Neutral theory-based estimates of extinction rates agree well with data for large areas ($1–10^3 \, km^2$, in Halley and Iwasa 2011). However, immigration, isolation, behavioral shifts and environmental stochasticity are likely more relevant in small fragments, in which cases the neutral model is likely to underestimate relaxation times (Halley and Iwasa 2011). In very large fragments, immigration and endemicity may explain overestimates provided by the neutral model (Halley and Iwasa 2011). In summary, understanding extinction debts depends on integrating the principles of a variety of theories and the mechanisms evoked by these theories. The relative importance of any of them is, most likely, case-dependent.

An important asset of theoretical models, particularly computational models, is that they make it possible to explore aspects of extinction debts that are difficult to quantify in real systems. For example, the evolutionary history of a trait can generate an extinction debt if the population ceases to adapt once evolutionary pressure decreases (Osmond and Klausmeier 2017). At the ecosystem-level, the loss of species interactions and ecosystem functions can happen more rapidly than species extinctions (Valiente-Banuet et al. 2015). Scaling up to ecosystem services, habitat destruction is estimated to have generated a debt of carbon storage loss ranging from 2 to 21 pentagrams of carbon (Isbell et al. 2015) this means that the global value of conserving vegetation for carbon storage ranges from US$0.3 to 3.1 trillion (and possibly higher values due to the uncertainties involved in
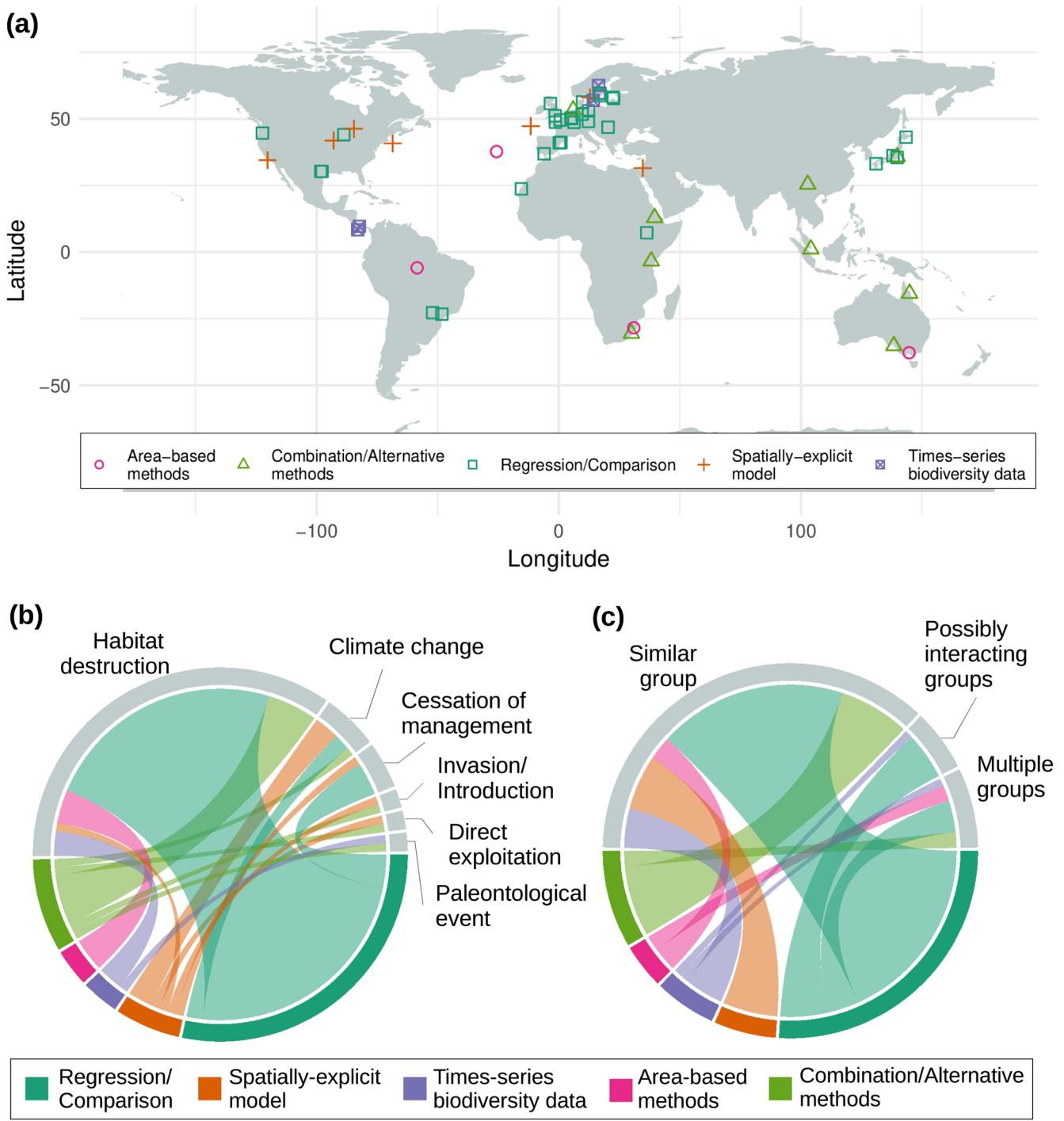
Figure 3. Distribution of (a) methods applied in each study detecting extinction debt, choice of methodology according to (b) perturbations generating the extinction debt, and (c) functional groups of the species for which the debt was analyzed. In panel (c): 'Similar group' refers to functionally similar species (e.g. 'plants' in Dullinger et al. 2012); 'Possibly interacting groups' refers to species that can possibly interact, meaning that extinctions in one group, would likely affect the other (e.g. 'plants' and 'butterflies' in Guardiola et al. 2018); 'Multiple groups' refers to species of different functional groups, for which the consequences of extinctions to interactions between the species are not necessarily considered (e.g. 'plants', 'bryophytes', 'mammals', 'reptiles', 'dragonflies', 'grasshoppers' in Dullinger et al. 2013). Panel (a) includes 58 empirical studies investigating extinction debts in real-world systems, published between 2009 and 2017. All studies are listed in Supplementary material Appendix 1 Table A1 (studies at the continental (n = 2), global (n = 4) or microcosmic (n = 1) scales were not included). Supplementary material Appendix 1 Fig. A2c shows the distribution of studies in Europe. Panels (b) and (c) include all 65 empirical studies.

these estimates; Isbell et al. 2015). Adding to this picture, extinction debts have been shown to decrease the sustainability of socio–ecological systems (Lafuite and Loreau 2017, Lafuite et al. 2017), reinforcing the consensus about the importance of biodiversity in providing ecosystem functions and services that benefit humanity (Cardinale et al. 2012, Hooper et al. 2012).

Methodological work

Species–area relationships (SARs) and endemics–area relationships (EARs) are two of the main methods for estimating extinctions following habitat loss (Kuussaari et al. 2009; hereafter referred to as 'area-based methods'). The SAR describes the number of species occurring in an area A. The EAR gives the number of species restricted to area a, which is part of A. 'Backward estimates' are done by comparing the SAR for current area and species richness and the SAR for past area and species richness (Kuussaari et al. 2009). The difference between current species richness and the value expected from the SAR for past conditions provides an estimate of the debt to be paid (Kuussaari et al. 2009). The EAR can also be used to predict the number of species likely to go extinct immediately after perturbation. The adequacy of such area-based methods, however, has been debated. Concerns include the possibility of overestimating extinction rates (He and Hubbell 2011, but see response by Axelsen et al. 2013), the possibility of underestimating extinctions (Halley et al. 2013, Chase et al. 2018) and the absence of uncertainty estimates and information on individual species extinction risks (Kitzes and Harte 2014).

Some studies explicitly investigated the mechanisms that could potentially generate under- and overestimates of extinctions (Supplementary material Appendix 1 Table A3). At least two area-based methods seem necessary to describe the dynamics of extinctions (Rybicki and Hanski 2013, Halley et al. 2014). One SAR is necessary to describe the relationships in a habitat before area loss and to predict immediate extinctions, caused by the loss of connectivity between patches (Halley et al. 2014). The other SAR is necessary to describe the relationship observed after habitat loss and to predict the total number of extinctions (Halley et al. 2014). Rybicki and Hanski (2013) attribute these two roles to a continental SAR (sampled from subareas of a continuous landscape) and to an island SAR (sampled from discrete habitat fragments). Although designed to estimate immediate extinction, EARs fail to account for short-term extinctions, which though not immediate, still happen soon after perturbation (Rybicki and Hanski 2013). All studies also highlight how the incorporation of ecological features, such as minimal population size (Tanentzap et al. 2012, Kitzes and Harte 2014), dispersal (Rybicki and Hanski 2013), immigration (Halley et al. 2014), or coexistence (Matias et al. 2014) can improve estimates. Considering the temporal and spatial extent to which habitat destruction can progress (e.g. Triantis et al. 2010 report > 95% habitat loss over 600 yr in

the Azores islands), the scales at which the different processes emerge must be addressed as essential aspects for the study of extinction debts.

Spatio–temporal scales of extinction debts

Extinction debts generated by anthropogenic perturbations (habitat destruction, climate change, species invasion, change in management and fishery – Fig. 2b) have been investigated in remnant habitat areas measuring from 0.013 to 5.5×10^6 km^2 (Fig. 4, Supplementary material Appendix 1 Table A4). The duration over which debts have been sustained varies from 5 to 570 yr, and projections of the total period required to settle a debt can extend to 1000 yr (Fig. 4, Supplementary material Appendix 1 Table A4). As the most investigated group, plants are well represented at all scales (Fig. 4a). Global values of the half-life of extinction debt and time to first extinction (Box 1) increase with remnant area for vertebrates, plants and less strongly for invertebrates (Halley et al. 2016).

The spatial scale at which to investigate extinction debt can determine whether or not they are detected. Reasons for this scale effect include 'purely' spatial factors, such as sample availability and correlations between explanatory variables (Krauss et al. 2010) and landscape context (Ernoult and Alard 2011, Guardiola et al. 2013, Alignier and Aviron 2017, Koyanagi et al. 2017). Additionally, this scaling issue may be a result from 'spatial scale-varying' mechanisms, such as faster extinction at smaller scales (Cousins and Vanhoenacker 2011, Guardiola et al. 2013) and species' sensitivity to perturbation (Cusser et al. 2015).

The relative abundance distribution and spatial aggregation of individuals influence the magnitude of extinction debts and the duration of relaxation times, as highlighted by neutral models (Halley and Iwasa 2011, Kitzes and Harte 2015, Chen and Shen 2017, Sgardeli et al. 2017). Communities following the lognormal and broken-stick abundance distributions tend to exhibit extinction debt following habitat decrease, especially under conditions of low aggregation of individuals. Following destruction of contiguous fractions of habitat, a higher aggregation of individuals can result in more immediate extinctions, smaller extinction debts and shorter relaxation times (Claudino et al. 2015, Kitzes and Harte 2015, Sgardeli et al. 2017).

While most studies of natural systems detect the 'age' of an extinction debt, i.e. the length of time since its causative perturbation, those that estimate or predict its duration are rarer (Supplementary material Appendix 1 Table A4). Moreover, some extinction debts are evaluated based on measures describing environmental conditions in periods that do not necessarily match the beginning (the measure is taken many years after it) or the frequency of perturbations (Supplementary material Appendix 1 Table A4). These studies often note that the data on past conditions used to infer extinction debt approximate those occurring before the most
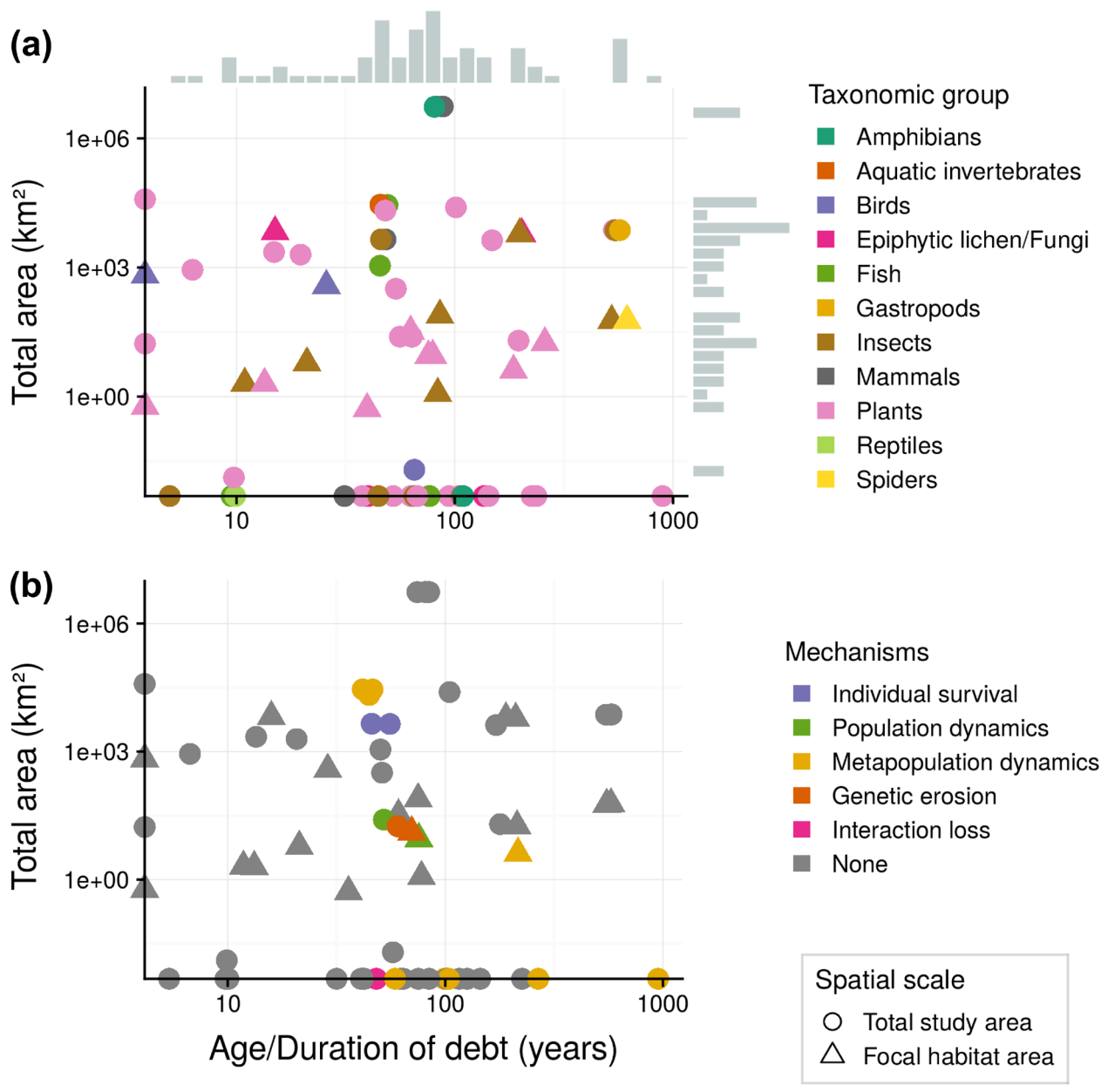
Figure 4. Spatio-temporal scales of extinction debts for (a) the organisms for which a debt was detected, and for (b) the mechanisms investigated. The spatial extent of the study was quantified as either the total area covered by the study, the total area of the focal habitat, or the total sampled area. Circles represent studies for which we could only approximate the total area of study. The relative sizes of focal habitat area and matrix inside the total area can vary wildly in these cases and are either hard to estimate from the provided maps or not available. Studies for which the total or the sampled area of focal habitat was identified are represented by triangles. These measures are closer proxies to the area actually 'paying' the debt. The age of debt refers to the time passed since the causative perturbation, while the duration refers to the time predicted or measured for a debt to be completely settled. Studies for which the spatial or temporal scales were not available or could not be derived are plotted in the x and y axes, respectively. The complete list of papers for which we were able to identify the spatial and/or temporal scales and their values is available in Supplementary material Appendix 1 Table A4.

important perturbation. In studies aiming at detecting extinction debts through regression techniques, such an approach is sufficient (Cristofoli et al. 2010; see Supplementary material Appendix 1 Table A4 for the complete list). However, the frequency of perturbations, rather than their magnitude, has a stronger impact on the size of extinction debts generated (Claudino et al. 2015). Therefore, it is worth further investigating the impacts of perturbation frequency on extinctions.

Mechanisms generating and delaying extinctions debts

Two mechanisms generating extinction debts have been explicitly investigated in real-world systems: 1) life-history traits that prolong individual survival, and 2) population and metapopulation dynamics that maintain sink populations under deteriorated conditions (Supplementary material Appendix 1 Table A1, A2 list all empirical and theoretical studies, and the mechanisms they address). We also discuss genetic erosion, as its occurrence during relaxation time has also been addressed. However, we do not frame genetic erosion itself as a mechanism of extinction debt (i.e. it does not delay extinctions), but rather as a component of it, resulting from the two mechanisms presented above and increasing extinction risk. Hence, genetic erosion accelerates the payment of the debt. For all three of these processes, we identify the spatio–temporal scales at which they have been studied (Fig. 4b). Below, we detail the evidence for each of these processes.

Individual survival: the role of life-history traits

Life-history traits, such as dispersal ability, reproductive strategy and longevity are often considered potential causes both of detected (Dullinger et al. 2013) and undetected extinction debts (Lundell et al. 2015, Hu et al. 2017, Roberts et al. 2017). The prevalence of clonality among remnant species indicates that asexual reproduction likely delays extinctions (Dullinger et al. 2012, Otsus et al. 2014). Trait trade-offs might also help to identify species most likely to be the first to pay extinction debts (Lindborg et al. 2012, Marini et al. 2012, Purschke et al. 2012, McCune and Vellend 2015, Saar et al. 2017). By the end of relaxation time, plant species with long-distance dispersal ability (e.g. wind-dispersal), but lower competitive and stress–tolerance abilities, were likely to have become locally extinct (Saar et al. 2012). Persistent species tend to be long lived and to reproduce clonally (Purschke et al. 2012, Saar et al. 2012). Assessments of such trait associations in the context of extinction debts among other guilds, however, are lacking, especially at higher trophic levels (Fig. 4a–b). Efforts to describe change in community trait composition (not necessarily restricted to life-history traits) should elucidate whether or not such changes can serve as early signs of population decline (Baruah et al. 2019), especially if those traits respond at similar temporal scales (Takkis et al. 2013). Detection of trait changes may also identify the role of microevolutionary processes in the payment of debts (Fagan and Holmes 2006, further discussed below).

Population and metapopulation dynamics maintain populations under deteriorating conditions

Extinction debts arise from population dynamics due to reduced seedling recruitment (Botzat et al. 2015, Plue et al. 2017), rate of succession (Lehtilä et al. 2016), local dynamics of competition and colonization (Duplisea et al. 2016).

Population dynamics have also been investigated together with genetic erosion (Fig. 4b, 5b). These studies illustrate how both processes may occur at similar temporal scales (Fig. 4b, but see Takkis et al. 2013), even if different life stages contribute differently to the build up of an extinction debt (Plue et al. 2017).

Metapopulation dynamics, i.e. local extinctions and re-colonization of populations connected by long-distance dispersal, are especially important in scenarios where habitat configuration (patch area and connectivity) is perturbed (Ovaskainen and Hanski 2002, Vellend et al. 2006). Special attention should be given to species remaining in habitat relics, since lack of connectivity between local populations may condemn a metapopulation in the long term (Wynne et al. 2014).

Metapopulation models have also been used to address extinction debts generated by types of perturbations beyond habitat fragmentation, such as species invasions (Gilbert and Levine 2013) and by climate change (Dullinger et al. 2012, Talluto et al. 2017). In the latter, metapopulation and species distribution models were combined (hybrid species distribution models) to predict range shifts; these can be interpreted as generating extinction debts at the trailing edge, and colonization credits at the leading edge (Pandit et al. 2017, Talluto et al. 2017). Because metapopulation and hybrid species distribution models are commonly used, they provide appropriate tools for generating explicit information about extinction dynamics. Moreover, colonization and extinction also depend on the species' life-history traits. Therefore, data-driven metapopulation models (Talluto et al. 2017) are particularly useful in accounting for the role of species' dispersal ability (Dullinger et al. 2013, May et al. 2013), colonization/extinction rates (Talluto et al. 2017), and eco-evolutionary dynamics (Cotto et al. 2017) in delaying both local and metapopulation-wide extinction.

Genetic erosion becomes increasingly important for smaller, often clonal populations

While is it possible that fragmented populations can maintain high genetic diversity (Habel et al. 2015), life history traits and life stages that delay extinctions usually decrease genetic diversity over the long term. Long lifespans and clonal reproduction make prolonged survival possible under deteriorated conditions (Cotto et al. 2017, Hu et al. 2017). However, clonal reproduction decreases genetic diversity (Jimenez-Alfaro et al. 2016, Hu et al. 2017) and long lifespans limits adaptive capacity (Cotto et al. 2017). It is also possible that even if pre-perturbation levels of recruitment are maintained, the genetic diversity of seed banks becomes lower than that of adult plants (Vranckx et al. 2012, Plue et al. 2017) contributing to a genetic extinction debt (delayed loss of genetic diversity). At the same time, the seed bank can also marginally contribute to prolongation of this debt by reintroducing alleles lost by the adult population (Plue et al. 2017). In perennial species, offspring maladaptation and consequent population decrease, can occur more rapidly than range losses
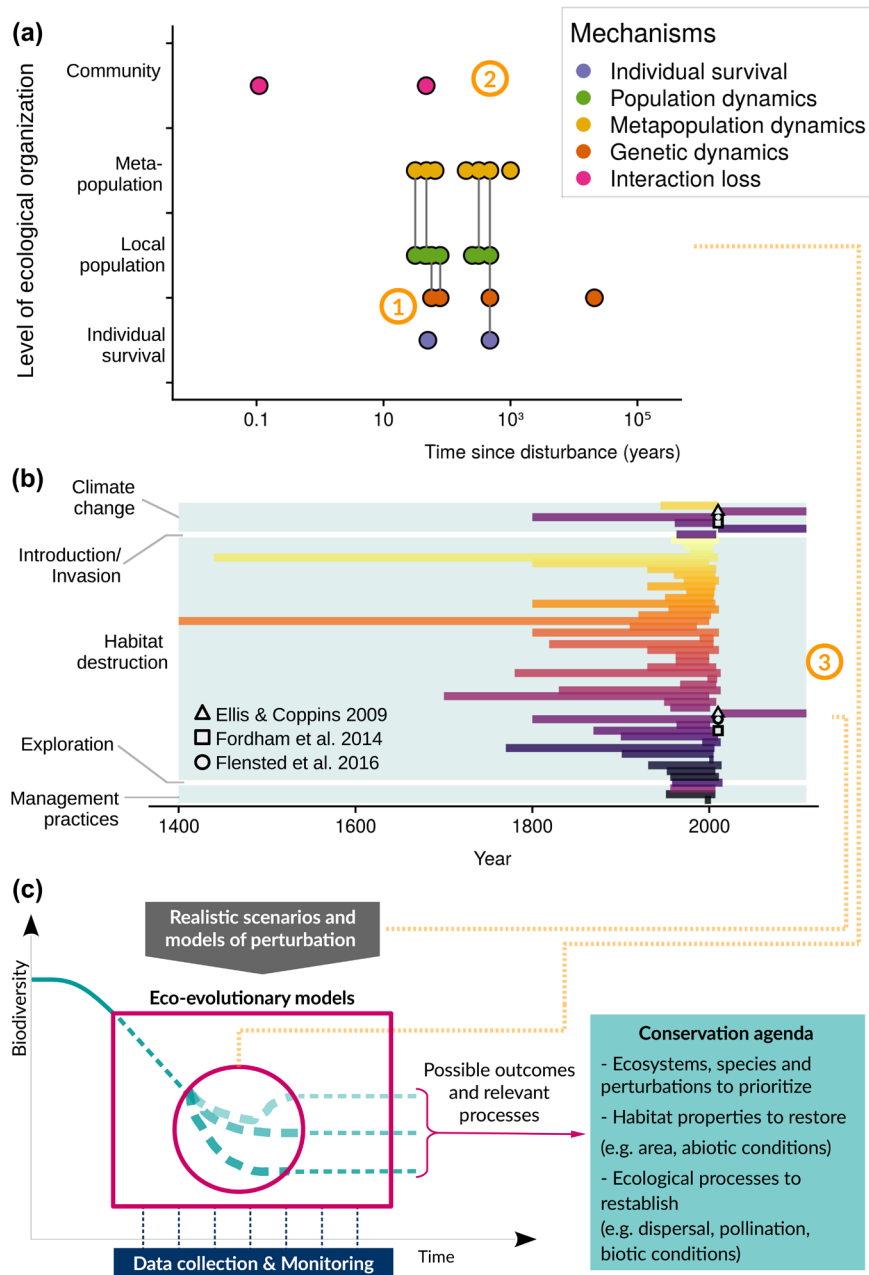
Figure 5. Roadmap for future research on extinction debt. (a) Ecological mechanisms investigated in scenarios of extinction debt plotted according to the ecological organizational level at which they were measured and the time scale of the debt. Studies included are the empirical studies which explicitly investigated ecological processes (n = 15; Supplementary material Appendix 1 Table A1) and Cotto et al. (2017), the only mechanistic model that was verified by empirical data (Supplementary material Appendix 1 Table A2). Lines connecting points indicate a single study that addressed more than one mechanism. Unconnected points represent studies that addressed only one mechanism. The paucity of studies addressing the microevolutionary dynamics of evolutionary processes (orange circle 1) and processes above the meta-population level, namely the disjunctive loss of interacting species (orange circle 2), justify our choice of these factors to integrate our roadmap. (b) Causative perturbations resulting in extinction debts identified in the empirical work and the age (time since perturbation) or duration of the extinction debt they generate. This panel summarizes empirical work for which we were able to assign one (or multiple) causative perturbations and an estimate of the age or duration of the debt (n = 49, listed in Supplementary material Appendix 1 Table A4). Studies reporting debt lasting more than 1000 yr were excluded to facilitate visualization. Studies are identified by color. Even though there is temporal overlap of different perturbations, few studies (n = 3, identified by different symbols) have included multiple sources of perturbations in their evaluation of extinction debts. For that reason, we included the impact of multiple regimes of perturbation on the payment of extinction debts (3) as the third avenue of our roadmap. (c) Eco-evolutionary models can provide better assessments of which ecosystems and species are critical to protect, perturbations that require priority action, as well as which abiotic and/or biotic conditions must be restored or reestablished to avoid future extinctions and waive the debt. Data collection and monitoring of model predictions are crucial to validate the models and to verify the efficiency of conservation measures.

(Dullinger et al. 2012, Cotto et al. 2017). The late loss of populations due to stochasticity and low genetic variability has been dubbed a genetic Allee effect by Vercken et al. (2013). However, the role of genetic erosion requires further investigation because loss of genetic diversity might happen more quickly than and be decoupled from decrease in population size (as in Takkis et al. 2013). Therefore, conservation measures aimed at mitigating extinction debts should include potential loss of genetic diversity, since it adds yet another source of stochasticity, in addition to demographic and environmental sources (Ovaskainen and Meerson 2010).

In summary, individual survival combined with population and meta-population dynamics under new landscape configuration enable transient population persistence for long periods of time despite genetic erosion. Notably, species life-history traits play a role in each of these processes, with three consequences. First, the very traits that contribute to individual survival under pre-perturbation conditions can contribute to increased extinction risk. This reinforces propositions made by Hylander and Ehrlén (2013) that individual, population and meta-population processes result in extinction debts. Second, this hierarchy of ecological processes inhibits a clear separation of factors delaying extinctions, as the different mechanisms interact with one another. Moreover, genetic erosion resulting from population and metapopulation processes does not generate debts but can accelerate debt payment. Third, an adequate appraisal of the relative importance of extinction-delaying mechanisms requires explicit consideration of how these mechanisms interact with one another. In the next section, we propose how this can be achieved.

A roadmap for future research

Previous work by Kuussaari et al. (2009) and Hylander and Ehrlén (2013) has called for more research focusing on methodological development, careful long-term monitoring of species at different organizational levels and spatial scales, and comparative studies of the impact of different types and intensities of perturbations. Another shared perspective is the need to better understand the temporal dynamics of extinctions.

The importance of a cross-level view of biodiversity has been stressed by the IPBES report (2019), which summarizes trends of essential biodiversity variables (EBVs – ecosystem structure, ecosystem function, community composition, species populations, organismal traits and genetic composition; Pereira et al. 2013). Albeit varying differently according to the driver of change, taxonomical group, geographic region and habitat types, there is an overall decline in EBVs (IPBES 2019). Nonetheless, despite growing recognition of the importance of the impact of habitat perturbation on evolutionary dynamics (Legrand et al. 2017, Pelletier and Coltman 2018, IPBES 2019) and the extent to which extinction cascades can reach (Roopnarine 2006, Vieira and Almeida-Neto 2015), neither mechanisms has been explicitly investigated under scenarios of extinction debt. This scarcity of studies is

perhaps due to methodological and data-related difficulties in assessing microevolution and biotic interactions. Combined with system idiosyncrasies (e.g. species composition and relative abundance, habitat configuration, perturbation regime), the feedback between ecological processes at different organizational levels may generate non-linear responses (e.g. abundance decrease, loss of genetic diversity, interaction loss) that cannot be captured by static methods. It is worth investigating the extent to which mechanism-based predictions match the ones provided by statistic methods (e.g. the values reported in IPBES 2019). Therefore, though the detection of extinction debts remains essential, a bigger challenge in understanding extinction debts is how these processes interact with one another under different perturbed conditions. To address this challenge, we propose a roadmap for future research (Fig. 5) consisting of three main avenues: 1) the microevolutionary dynamics of extinction processes, 2) the disjunctive loss of interacting species and 3) the impact of multiple regimes of perturbations on the payment of extinction debts. The first two avenues address understudied processes happening during relaxation time, while the last avenue addresses an understudied aspect of extinction debt that would benefit from mechanistic understanding. We also briefly explore the potential contributions of these avenues to conservation measures (Box 2). Finally, we propose integrative mechanistic models as tools to navigate this roadmap.

1) The microevolutionary dynamics of extinction processes

Microevolutionary dynamics are especially relevant in reduced (and often clonal) populations, for the potential that genetic drift and inbreeding have to decrease populations' effective size and increase their extinction risk (Keller and Waller 2002, Spielman et al. 2004, Dixo et al. 2009, Hendricks et al. 2017). In such a scenario, extinction vortex is a theoretical construct used to illustrate the synergy between environmental, demographic and genetic factors that accelerates the descent of an already declining population towards extinction (Fagan and Holmes 2006, Blomqvist et al. 2010). Decreased genetic diversity detected during the payment of extinction debts can be interpreted as a sign of an extinction vortex (Vercken et al. 2013). We propose that extinction vortex and extinction debt could be addressed as two complementary phenomena. First, the synergy between environmental, demographic and genetic factors, i.e. the onset of the extinction vortex, takes time to happen and delays extinctions. The more deeply populations are drawn into the vortex (as they pass the extinction threshold, and/or lose genetic diversity), the more rapidly extinction rates become. Second, the extinction vortex was conceived for application to a population, while an extinction debt exists at the metapopulation or community level. This implies that population-level extinction vortexes could reinforce each other and affect the payment of extinction debts. Therefore, the reinforcement of extinction vortexes themselves is another synergistic factor that complicates our understanding of extinction dynamics.

Box 2. Mechanistically informed conservation

The potential to identify future extinctions is one of the main assets of the extinction debt concept. We illustrate how policy management could integrate mechanistic knowledge to realize this potential. For this, we work on a fictive case of an extinction debt for habitat–specialist plant species caused by habitat fragmentation. Knowledge of the current trait composition of the remnant species is crucial to identify which are at most risk of going extinct to settle the debt. In our example, let's assume non-clonal, wind-dispersed plants are still present, but can be expected to go extinct as the debt is settled (Saar et al. 2012). This information allows identifying which ecological processes are affected by the causative perturbation. It is important to account how ecological processes are affected by the perturbation and how they respond to conservation measures.

If non-clonal, wind-dispersed species are likely to become extinct, it is possible to identify ecological mechanisms contributing to the extinction process:

A) At the metapopulation scale, the possible fates – adapt or perish – of a species, particularly if habitat specialist, can be particularly dependent to dispersal. For example, loss of connectivity in a highly fragmented landscape might indicate the highest extinction risk (Saar et al. 2012), whereas preservation of minimal connectivity may actually make population rescue possible (Huth et al. 2015). In the first case, artificial sowing or increase in connectivity may decrease extinction risk. In the second, simply maintaining the current connectivity might be enough.

B) At the local scale, competition with generalist or invasive species can increase extinction risk. Management practices would involve electrical mowing or pasture grazing to minimize fitness differences from stronger competitors. This might be crucial in conserving our example species, as by the colonization–competition trade-off, wind-dispersed species can be expected to have lower competition ability. Combined with the lower colonization success under a highly fragmented landscape, propagule pressure of dispersing seeds might not be enough to withstand the competition anyways. Therefore, increasing of dispersal rates would be ever so important.

C) Other possibilities of improving survival would tackle the reproductive success of remnant species. Reintroducing pollination services for non-clonal species could increase their recruitment rates. This, however, requires careful choice and timing of the pollinators to be used and the possible impacts on wild pollinators.

The three mechanisms A, B and C are not isolated, but their relative importance will depend, among other factors, on the trait composition of the remaining populations, on the relative abundances, habitat configuration and pollination availability. Moreover, the relative importance of these mechanisms will likely also vary during the time since perturbation. In this case, a metapopulation model with explicit dispersal functions can help identify which strategy illustrated in A or B (if it is a trade-off model) would be more efficient. If it is possible to increase complexity, metacommunity models including species interactions would provide possible alternatives of management (strategy C). Moreover, if including evolutionary dynamics, such models could even illuminate unforeseen consequences of the relaxation process (Cotto et al. 2017).

Characterizing populations decline (Fagan and Holmes 2006) when debts are being paid could verify these predictions and potentially indicate when this synergy is triggered at the community level (Fig. 5a).

It is also possible that, during relaxation time, adaptive dynamics save populations from extinction via selection of traits adapted to the new conditions, i.e. 'evolutionary rescue' (Gomulkiewicz and Holt 1995). In these instances, at least part of the debt could be waived. Although not yet empirically verified, theoretical results illustrate the complexity of the phenomenon. On the one hand, it is possible that trait evolution before perturbation pushes trait values in directions contrary to rescue, hampering rescue as a result (Osmond and Klausmeier 2017). On the other hand, genetic drift in small populations may actually facilitate evolutionary rescue from evolutionary suicide (i.e. an evolutionary attractor that becomes a disadvantage under environmental change – Ferriere and Legendre 2013). For microbial populations, the conditions necessary for evolutionary rescue vary (Bell and Gonzalez 2011, Bell 2013), but genetic variation and population size are critical. For larger organisms, the question remains whether partial waiving of extinction debts via

evolutionary rescue is possible. Longer generation times, combined with genetic erosion, low population sizes, and demographic and environmental stochasticity, have been shown to hamper evolutionary rescue in vertebrate species (Vander Wal et al. 2013). Unfortunately, studies of evolutionary rescue in wild populations are rare due to demanding data requirements (Vander Wal et al. 2013). Although evolutionary rescue in wild populations is possible (Vilà et al. 2003), its likelihood of occurring (Vander Wal et al. 2013) and its actual role in conservation biology (Hao et al. 2015) are still under discussion, requiring further research. The competition–colonization trade-off may be a good candidate for exploring such dynamics. This trade-off is often studied in contexts where change in landscape configuration affects the outcome of competitive interactions (Chen et al. 2009, Orrock and Watling 2010, Mouquet et al. 2011 – detailed in Supplementary material Appendix 1 Table A2), but it may also play a role in determining the outcome of eco-evolutionary dynamics (Legrand et al. 2017). For example, evolutionary decrease in dispersal propensity at the local scale (in response to habitat amelioration) can increase metapopulation extinction risk (Poethke et al. 2011).

2) The disjunctive loss of interacting species

Considered under the network paradigm, extinctions can lead to extinction cascades (Emer et al. 2018), decreases in community stability (Spiesman and Inouye 2013) and even network collapse (Jiang et al. 2018). Although the importance of accounting for secondary extinctions is firmly recognized (Brodie et al. 2009, Colwell et al. 2012), the contribution of cascading effects to the payment of extinction debts remains the least explored component of extinction debts. In our search, we found only microcosm experiments by Gibbs and Jiang (2017), a theoretical model of extinction debt of ecological interactions by Valiente-Banuet et al. (2015) and an empirical study of interaction network change in a scenario of extinction debt by Guardiola et al. (2018) (Fig. 4b, 5a).

Network sciences in ecology are still in development (Borrett et al. 2014, Pilosof et al. 2017, Delmas et al. 2019). Analyses of temporal networks (Masuda and Lambiotte 2016) and network robustness are particularly important (Grass et al. 2018, Guardiola et al. 2018), since species go extinct at different rates during relaxation time. In this context, plant–herbivore and plant–pollinator communities represent good model systems, since plant populations promote community stability by connecting pollination and herbivory networks (Sauve et al. 2016) and differential responses of pollinators and herbivores to perturbation have contrasting effects on community maintenance (Georgelin et al. 2015).

Because extinctions take time to happen, we propose going beyond robustness analyses, which assume sudden extinction, and breaking down the progressive feedbacks between ongoing extinction processes in populations of interacting species during relaxation time. Species interactions are the result of spatial and temporal matching of species occurrence, population abundances and interaction traits (Thompson 2010, Poisot et al. 2015). These factors can all be affected as a debt is paid. During relaxation time, interacting species go extinct at different rates (Bommarco et al. 2014, Cusser et al. 2015, Guardiola et al. 2018) affecting presence and abundance matching. The loss of species interactions could be a particularly important factor behind extinctions caused by climate change (Cahill et al. 2012). Even before extinctions happen, continuous and directional perturbations such as climate change can induce phenological shifts between interacting species that alter population dynamics and community stability (Fabina et al. 2010). As we proposed in the previous subsection, it is also worth investigating whether microevolutionary processes in small populations may generate a mismatch in interaction traits. Additionally, it is possible that there is not enough time for microevolution to allow species to adapt to new conditions before it gets excluded by an invading preadapted one (Holt 1990). Therefore, evolutionary rescue and interaction networks should be studied in the context of changes in both abiotic and biotic conditions.

Beyond the change in species interactions and in biotic conditions, ecosystem functions and services can also be lost more rapidly than the extinctions occur (Valiente-Banuet et al. 2015) and feedback into ongoing extinction processes, generating nonlinear biodiversity responses (Essl et al. 2015a). Tackling these confounding effects in empirical settings is challenging (Essl et al. 2015a), especially due to the experimental complexity required. Nonetheless, these intertwined processes (i.e. evolution, environmental change and metacommunity dynamics) should be more easily disentangled in theoretical studies utilizing mechanistic models that can integrate all these mechanisms simultaneously (Schiffers et al. 2013, Cabral et al. 2019, see also Cabral et al. 2017 for a review of such integrative biodiversity models).

3) The impact of multiple regimes of perturbation on the payment of extinction debts

The concept of extinction debt relies on the perturbation of a community at an equilibrium state, leading to relaxation at another equilibrium state. However, the Anthropocene brings a series of simultaneous threats to biodiversity (e.g. climate change, invasions, fragmentation – Bowler et al. 2018, IPBES 2019, Fig. 2b shows the causative perturbations included in this review and Fig. 5b illustrates their co-occurrence) that are likely to reinforce each other (Brook et al. 2008). This means that relaxation processes themselves are perturbed and the new equilibrium is delayed or constantly shifted. Regardless of the idiosyncrasies of relaxation processes, which are likely case-dependent, current biodiversity loss is happening rapidly. Current extinction rates have been calculated to be between 10 and 1000 times the background rate for vertebrates (Pimm et al. 2014) and up to 500 times for plant species (Humphreys et al. 2019). Current anthropogenic drivers of biodiversity change include land/sea use change, pollution, direct exploitation, species invasions and climate change (IPBES 2019). The effects of varied regimes (types and frequency) of perturbation on the extinction dynamics of the same system have been addressed in mechanistic modeling studies and microcosm experiments (Claudino et al. 2015, Gibbs and Jiang 2017, Zarada and Drake 2017), but not verified in real-world systems. Because the relative incidence of various perturbations also varies in space and time, any cross-system comparisons (including meta-analyses) require adequate replicate sites undergoing similar combinations of perturbations and must control for confounding effects (Bowler et al. 2018 characterize and provide such threat complexes at the global scale).

Mechanistic simulation modeling as a navigational tool

When addressing extinction debts, simulation-based models have been used to predict relaxation times (May et al. 2013), to verify the impact of different perturbations on the size of extinction debts (Claudino et al. 2015), to test theoretical assumptions (Halley and Iwasa 2011, Huth et al. 2015), and to verify the effectiveness of conservation measures (Wearn et al. 2012, Fordham et al. 2016). They have also proved to be useful, yet underused, tools for investigation of the impacts

of climate change and species invasions (Cahill et al. 2012, Gilbert and Levine 2013). Our knowledge of how eco-evolutionary processes lead to delayed extinctions and the full extent of their feedbacks (Legrand et al. 2017) and ecosystem-level consequences (Valiente-Banuet et al. 2015) is still incipient. Simulation models can integrate all those processes (Thuiller et al. 2013, Urban et al. 2016, Cabral et al. 2017) and fill the gaps. An example is Cotto et al. (2017), an eco-evolutionary model used to investigate extinction debt and able to connect processes at the individual, population and metapopulation levels (Fig. 5a). Such an approach is especially useful for informing conservation efforts (Wood et al. 2018), which may currently overlook delayed extinctions (Urban 2015, Chen and Peng 2017 – see Box 2 for considerations of conservation policies). Specifically, accounting for extinction debt when planning conservation and management has been shown to be especially useful when funding is limited; knowledge of the dynamics of extinctions allows more effective resource allocation (Leroux et al. 2009, Leroux and Whitten 2014, Iacona et al. 2017). Considering the spatio-temporal scales that extinction debts can reach (Fig. 4, Halley et al. 2016, 2017), further investigation into their consequences, and the extension of those consequences to ecosystem service debts (Isbell et al. 2015, Valiente-Banuet et al. 2015, Lafuite and Loreau 2017, Lafuite et al. 2017) is essential if we are to understand extinction debt implications for human life (Isbell et al. 2017). At the same time, the more mechanistically complex a model is, the harder it is to parameterize (Getz et al. 2018) and to interpret emergent patterns. In that context, as previously mentioned by Kuussaari et al. (2009) and Essl et al. (2015a), integrative long-term studies are essential to constrain parameter values and model assumptions (i.e. neutral versus niche-based dynamics) as well as to evaluate emergent patterns (Haddad et al. 2015, 2017). Moreover, adaptive modeling strategies can guide data collection as well as improve prediction accuracy (Urban et al. 2016). Integrated with systematic model testing and revision (Urban et al. 2016), such long-term biotic and abiotic monitoring could further support robust assessment of the full impact of habitat perturbation, from loss of species to loss of interactions and ecological functions (Ojanen et al. 2013, Dirzo et al. 2014, Haddad et al. 2015, Valiente-Banuet et al. 2015).

Conclusions

Our review demonstrates an increasing effort to understand the mechanisms involved in extinction debts across systems and scales. To date, the contributions of niche-based, neutral and metapopulation dynamics have been fairly well characterized. Evolutionary and biotic interaction processes, however, remain less adequately addressed and thus deserve further inquiry. To this end mechanistic models make it possible to scale individual responses to the population and metapopulation levels and to better characterize feedback processes. The roadmap to improve our understanding of extinction debts includes entraining genetic dynamics into the prediction

of (meta)population dynamics, scaling cascading effects to the community level, and studying the combined effects of different types of perturbations. While long-term empirical studies of community dynamics and underlying drivers of extinctions remain important to monitor biodiversity change, and to calibrate and validate model-based forecasts of extinction debts, it may be too late to counteract severe losses of biodiversity. Hence, immediate policy and conservation efforts must consider mechanisms of extinction debt explicitly in order to preserve remaining biodiversity in a rapidly changing world.

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